ADULT NOCTUIDAE FEEDING ON APHID HONEYDEW AND A DISCUSSION OF HONEYDEW FEEDING BY ADULT LEPIDOPTERA¹

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ABSTRACT. Adult Aseptis characta (Grote) and Rhynchagrotis exertistigma (Morrison) (Lepidoptera: Noctuidae) were observed feeding on honeydew produced by Zyxaphis canae (Williams) (Homoptera: Aphididae) on basin big sagebrush, Artemisia t. tridentata Nuttall, in south-central Idaho. The feeding behavior is described. The lack of similar reports among other Lepidoptera, excluding the Lycaenidae, is discussed. Means by which the moths could locate honeydew sources and the adaptive value of this ability in specific situations are considered.

On 22 July 1983, a male Aseptis characta (Grote) and a female *Rhynchagrotis exertistigma* (Morrison) (Lepidoptera: Noctuidae) were observed feeding on the honeydew of *Zyxaphis canae* (Williams) (Homoptera: Aphididae) on basin big sagebrush, Artemisia t. tridentata Nuttall. This observation was made in a canyon 6 miles SSW of Howe, Butte Co., Idaho. The day was moderately cool (about 22°C) and cloudy, with a light rain falling. Despite the weather, there was a moderate amount of insect activity. Numerous aphids, flies and wasps, especially Ichneumonidae, were seen on the sagebrush, Artemisia spp.

Each moth located an aggregation of aphids and moved its proboscis from aphid to aphid within that aggregation. Then, each probed with its proboscis and if necessary, walked a short distance to locate another group of aphids. The behavior was similar to locating composite inflorescences and probing individual florets.

Feeding on homopterous honeydew is a logical extension of the typical nectar-feeding habit of adult Lepidoptera. Both are aqueous solutions containing carbohydrates and amino acids, plus a variety of minerals, lipids, organic acids and vitamins (Hagen, 1958; Auclair, 1963; Strong, 1963; Baker, 1977; Baker & Baker, 1979). Nectars may also contain potentially toxic compounds, e.g. alkaloids and glycosides (Baker, 1977; Baker & Baker, 1979). There are no reports of such potentially toxic compounds in honeydews. Therefore, it should be possible for many adult Lepidoptera to exploit this alternative food source. However, few accounts of honeydew feeding by adult Lepidoptera could be located and all involved Lycaenidae (Bingham, 1907; Lamborn, 1914; Roepke, 1918; Farquharson, 1922; Balduf, 1939; Hin-

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ton, 1951; Gilbert, 1976; Orsak, 1977; Henning, 1983). Species in some lycanenid genera are not known to visit floral nectaries, so homopteran honeydew may be their primary source of nutrients (Cottrell, 1984).

All of the earlier reports of adult Lepidoptera feeding on homopterous honeydew involved Lycaenidae. The family includes many, taxonomically diverse species in which the larvae are predaceous on Homoptera, associated with ants in some way or both (Balduf, 1939; Clausen, 1940; Hinton, 1951; Henning, 1983). Species with homopterophagous or myrmecophilous larvae commonly oviposit near aggregations of Homoptera which serve as prey or indicators of an area where hosts are likely to be found, respectively. Therefore, it is not surprising that they have evolved the habit of exploiting honeydew as a readily available source of adult food.

There is no evidence that A. characta or R. exertistigma would be expected to locate aphid aggregations for any purpose, other than as a source of honeydew. This implies that exploiting this alternative food source should be possible for many Lepidoptera, in addition to the entomophagous Lycaenidae. The paucity of observations of this behavior in other groups could be due to Lepidoptera being less conspicuous when feeding on honeydew than when feeding on nectar. Entomophilous flowers are usually prominently displayed so that they may be more readily located by their insect pollinators (Jensen & Salisbury, 1972). Most aphid aggregations, on the other hand, are relatively inconspicuous and may be effectively concealed, thus, also concealing any visitors. However, since many Lepidoptera are relatively large and easily observed, it seems unlikely that this behavior would not have been reported more frequently, if it were common. So, it seems probable that adult Lepidoptera, other than Lycaenidae, rarely consume honeydew.

At this point two questions arise: 1) Why is honeydew feeding unusual among adult Lepidoptera, other than Lycaenidae?; and 2) Why did it occur in the situation described earlier? Possible answers for both questions will be discussed.

While adult Lepidoptera are generally regarded as nectar-feeding insects, they actually display considerable flexibility in their feeding behavior. "Puddling," in the broad sense, includes feeding at the margins of puddles, etc. and on urine, dung and carrion (Arms, Feeny & Lederhouse, 1974; Downes, 1973); it is common among adult Lepidoptera. Some Lepidoptera are also known to feed on fluid from the eyes of mammals and mammalian skin secretions, including sweat, and blood flowing from wounds (Bänziger, 1971; Buttiker, 1959, 1962, 1964). Still more specialized is behavior of the SE Asian noctuid *Calyptra eustrigata* (Hmps.), which moth uses its proboscis to pierce the skin of large mammals to obtain blood meals (Bänziger, 1971, 1975). Water and amino acids were considered to be the key nutrients acquired from these atypical food sources, but in at least some cases, the acquisition of sodium may also be of great importance (Arms, Feeny & Lederhouse, 1974). The two latter nutrients could be deficient in specific nectars, therefore, these foods could be important supplements to diets that consist largely of nectar. In this situation, it is not surprising that Lepidoptera have evolved the habit of exploiting these food sources.

Still, some adult Lepidoptera regularly consume atypical foods that would seem more suitable as substitutes for nectar, than as dietary supplements. African and Asian Sphingidae of the genus Acherontia, commonly enter nests of wild and domestic bees to consume stored honey (Balduf, 1939). Their probosces are recurved apically and relatively short, indicating that they may be specialized for feeding in this manner. Bänziger (1970) discusses a Malayan noctuid, Calyptra thalictri (Bkh.), that uses its similarly structured proboscis to pierce fruit. (This behavior is assumed to be ancestral to the skin-piercing, blood-sucking habit of C. eustrigata.) In these two cases, the high concentrations of sugars in the foods suggest that carbohydrates may be among the nutrients sought by the moths. The high sugar concentrations and the large volumes of food available in these situations seem to be plausible reasons for the moths evolving these unusual feeding habits. However, the possibility of some other nutrient(s) being of primary importance to the moths cannot be totally discounted.

Though few in number, these examples of highly modified feeding behaviors, which are apparently directed primarily to the acquisition of carbohydrates, are important. They make it more surprising that adult Lepidoptera do not consume homopterous honeydew more regularly. Intuitively, it would seem that there must be some factors which have tended to restrict their exploitation of this food source.

The Ditrysia, the dominant and most advanced suborder of the Lepidoptera, seem to have radiated ecologically and taxonomically, in synchrony with the Angiospermae (Common, 1970, 1975). With a coevolutionary history that extends back about 100 million years to the mid-Cretaceous (Powell, 1980), it is not surprising that these Lepidoptera have, in general, evolved the specialized ability to efficiently locate floral nectar sources using visual and olfactory cues (Brantjes, 1976).

An aggregation of aphids would certainly not present visual stimuli like those of a flower or inflorescence. Nor would there be any stimulus analogous to floral odor to guide Lepidoptera to a source of honeydew. Yet, the occurrence of Lepidoptera at sap flows on injured trees and the successful use of molasses bait traps, demonstrate that some Lepidoptera are capable of locating food sources using only olfactory cues other than floral odors. Therefore, it is possible that some Lepidoptera could locate honeydew sources, perhaps in a manner similar to that used by *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae). Adult *C. carnea* orient anemotactically to indole acetaldehyde, a breakdown product of the amino acid tryptophan which occurs in some honeydews (Hagen, Greany, Sawall & Tassan, 1976; van Emden & Hagen, 1976). So, the question remains, why is a convenient food source apparently underexploited by adult Lepidoptera?

Competition with ants and other common honeydew-feeding insects seems likely to be an important factor. Unlike floral nectar, which is often protected by morphological and chemical systems which restrict access to specific groups of visitors (Grant & Grant, 1965; Heinrich, 1970; Feinsinger, 1983), honeydew is usually exposed and freely accessible to many visitors. Therefore, the honeydew-feeding niche would be more likely to be dominated by groups like the ants, which are abundant, aggressive, effectively search plant surfaces and are less specialized in their feeding habits.

The generally ready and dependable availability of flowers during the seasons of adult Lepidoptera activity may be equally important. Aphid populations are prone to sudden, dramatic increases, e.g. pest outbreaks, and decreases, e.g. following an *Entomophthora* sp. epizootic (Hagen, 1976) or a period of extreme heat (Neuenschwander, Hagen & Smith, 1975). This less stable situation would seem poorly suited to relatively short-lived, pro-oogenic species, like most Lepidoptera (Chapman, 1982), which must rather quickly locate carbohydrate sources and deposit large numbers of already mature eggs. The influence of dependably available nectar is indirectly supported by the circumstances that existed at the time this observation was made.

In the high desert of south-central Idaho, mid-July is normally a time of transition, as the late spring flowers, e.g. desert paintbrush, *Castilleja chromosa* A. Nelson, globe mallow, *Sphaeralcea munroana* (Douglas) Spach ex Gray, and *Chaenactis douglasii* (Hooker) Hooker and Arnott, are passing and the summer flowers, e.g. rabbitbrush, *Chrysothamnus* spp. and horsebrush, *Tetradymia* spp. are coming into bloom. Sagebrush species in this area begin flowering in early fall and produce little, if any, nectar since they are anemophilous (Stebbins, 1974). However, in July 1983, an atypical, prolonged period of cool, rainy weather seemed to substantially delay the bloom of the summer flowering shrubs in this area, leading to a temporary, but acute, shortage of nectar sources.

Prolonged periods of moderately cool weather are also known to produce "aphid years." This is believed to be due to the temperature remaining above the developmental threshold of the aphid species, but

below that of their predators and parasites (Neuenschwander, Hagen & Smith, 1975). This situation can lead to a rapid increase in the aphid population. An increase of this type would have increased the availability of honeydew, thus, increasing the likelihood that the moths would discover this alternate food. Since it remained cool and rainv at the time this observation was made, the weather may have severely limited the moths' abilities to search for and exploit the few nectar sources that were available. It seems likely that some combination of these factors induced the moths' atypical behavior.

So, honeydew feeding by adult Lepidoptera, other than entomophagous Lycaenidae, appears to be uncommon. If it were generally to occur only under circumstances similar to those outlined above, it would explain the scarcity of reports of this intuitively logical behavior. Still, under specific conditions, the ability to efficiently locate and consume honeydew could be important to the survival of many Lepidoptera.

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